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Original Research

Combined effects of warming, snowmelt timing and soil disturbance on vegetative development in a grassland community

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Running headline: vegetative development in a warming experiment

Abstract

Climate warming and advanced snowmelt can simultaneously affect plant communities. However, the process of seasonal vegetative development under warming and early snowmelt conditions remains unclear, especially given that disturbance can amplify or dampen the effect of warming. This study addressed these issues using a 3-year experiment in a productive grassland in a cool temperate region. Three experimental conditions were established in the grassland: warming and early snowmelt using open-top chambers (OTCs), early snow removal and ambient temperature (SRs), and natural snowmelt and ambient temperature (CONTs). Half of the area of all plots was plowed to disturb soil conditions. Average temperature and snowmelt were 1.37°C higher and 16–26 days earlier in OTCs relative to CONTs, respectively. Vegetation censuses during the 1–4 week intervals showed earlier increases in species richness and vegetation cover after snowmelt in OTCs than CONTs and SRs. Differences in species richness and plant cover among treatments were substantially diminished in plowed areas. Aboveground biomass showed little difference among treatments at the end of the growing season, while richness remained higher in OTCs. These results indicate that early snow removal did not alter grassland vegetation. The effect of OTCs can thus be due to either warming or a combination of early snowmelt and warming. Although climate change is predicted to have strong impacts on arctic and alpine ecosystems, this study suggests that the warming may also have important impacts in temperate regions.

Key words: cool temperate; diversity; *Miscanthus sinensis*; open-top chamber; productivity; snow removal

Introduction

One possible consequence of global warming is earlier snowmelt (Barnett et al. 2005; IPCC 2013), which leads to an extended growing season for vegetation (Galen & Stanton 1995; Carbognani et al. 2012). Effects of global warming and early snowmelt increase the growth and reproduction of plants that experience warm temperatures and long-growing seasons (Henry & Molau 1997; Totland & Altalo 2002; Semenchuk et al. 2013). However, early snowmelt can expose vegetation to the risk of frost damage (Bannister et al. 2005; Gu et al. 2008; Inouye 2008) and disrupt plant–pollinator relationships (Kudo et al. 2004, 2008; Hegland et al. 2009). Therefore, the balance between positive and negative effects of warming and early snowmelt can result in optimal performance of plants under intermediate timing of snowmelt (Hülber et al. 2011).

A large number of experimental studies have examined the effect of warming on plant communities using open-top chambers (OTCs; Elmendorf et al. 2012). A potential problem of OTCs is that warming and early snowmelt often occur simultaneously when snow accumulation in OTCs is reduced (Aerts et al. 2004; Baptist et al. 2010). The effects of snowmelt timing have also been examined using snow manipulation experiments, in which the removal or addition of snow causing earlier and later snowmelt significantly altered community composition, species hierarchy, phenology, and the growth and reproduction of individual species (Wipf & Rixen 2010; Semenchuk et al. 2013; Rumpf et al. 2014). Although assessing warming and snowmelt timing independently in field studies is difficult, a field experiment with a combination of warming by OTCs and snow manipulation should allow one to evaluate the relative effects of both factors on vegetation development (Aerts et al. 2004, 2006).

Previous studies have focused on the effects of climate change on arctic and alpine ecosystems, which are characterized by low temperatures, a short-growing season, low productivity, low species diversity, and sparse plant density, and such ecosystems are expected to be very sensitive to climate change (Henry & Molau 1997; Arft et al. 1999; Elmendorf et al. 2012). As warming has relaxed the severe environmental conditions in cold biomes, the abundance of some plants, especially graminoids and shrubs, has increased, causing a loss of species diversity (Klein et al. 2004; Walker et al. 2006). In contrast, little research has investigated plant communities with high productivity, high plant density, high species diversity, and a long growing season in temperate regions. Moreover, communities disturbed by human impacts are expected to be more vulnerable to warming than undisturbed, natural communities (Grime et al. 2000). Anthropogenic disturbances are more frequent in low-altitude and temperate regions than in arctic and alpine regions (Hannah et al. 1995). Therefore, climate change may have major impacts on low-altitude and temperate regions.

To assess the combined effects of warming, snowmelt, and soil disturbance on the development of vegetation, I conducted a 3-year experiment in a productive grassland community dominated by Japanese pampas grass (*Miscanthus sinensis*) in a cool temperate, montane region. The region experiences cold temperatures and continuous snow cover during periods from early December to early April in every year (Yasunari & Ueno 1987). The objectives of this study were to compare the timing and magnitude of vegetation growth among three experimental conditions (warming and early snowmelt using OTCs; early snow removal and ambient temperature; natural snowmelt and ambient temperature) and to investigate whether soil disturbance amplifies or dampens the effects of warming and early snowmelt.

Materials and methods

Study site

The study site was located at the Sugadaira Montane Research Center, University of Tsukuba (36˚ 31' N, 138˚ 21' E), at an altitude of about 1,300 m on the Sugadaira plateau, Ueda-shi, Nagano Prefecture, central Japan. The annual mean air-temperature at the site was 6.5˚C and the average monthly air-temperature ranged from 19.4˚C in August to –5.6˚C in February, whereas the mean annual rainfall was 1,226 mm and the annual mean of maximum snow depth was 102 cm for the years 1971–2006.

A field experiment was conducted in a semi-natural grassland in the Sugadaira Montane Research Center during 2011–2013. The dominant plant within the grassland is Japanese pampas grass (*Miscanthus sinensis*), which is typical for mountainous areas in Japan. Every autumn, the facility manager harvests all of the aboveground plant parts, to maintain grassland vegetation by preventing vegetative succession to forest and to provide the litters to farmers for composts. More than 100 plant species, including seedlings of tree species, have been observed in the grassland.

Field experiment

This study established three experimental conditions in the grassland: warming and early snowmelt using open-top chambers (hereafter OTCs), early snow removal and ambient temperature (hereafter SRs), and natural snowmelt and ambient temperature (hereafter CONTs). The experimental design was not a factorial design due to the lack of an experimental condition with warming and natural snowmelt. To assess the effect of soil disturbance, a plowing treatment was assigned as a factorial design among the three conditions. Five OTC plots and five CONT plots were established in the grassland in November 2010. Five SRs plots, in which snow was removed according to snowmelt in OTCs, were added in November 2011. Each plot had an area of 1 m × 1 m, and half of the area of all plots was plowed in November 2012 to disturb the vegetation. Therefore, this study examined two experimental conditions in 2011 (OTCs and CONTs), three in 2012 (OTCs, SRs, CONTs), and six in 2013 (OTCs, SRs, and CONTs, with and without plowing). Open-top chambers were produced using stainless steel frames and corrugated, acrylic-transparent panels of 2 m height and 1 m width that surrounded all lateral sides (Plate 1). The 2-m height of panels was adopted to surround the maximum height of the vegetation that exceeds two meter in mid-September. The top and a region 10 cm above ground were opened in each OTC. OTCs remained on plots throughout the experimental period.

A temperature logger (Thermocron iButtons, DS1921G; Maxim Integrated Products, Sunnyvale, CA, USA) was installed at 1 m height in the center of each OTC and CONT plot by attaching an iButton to a standing pole., Each iButton was covered by a plastic cup to shade direct sunlight without preventing air circulation. Air temperatures were recorded in 1-h intervals from 1 January 2011 to 11 November 2012, and 2-h intervals (0, 2, 4, 6, 8, 10, 12, 14, 18, 20, and 22) from 29 November 2012 to 30 June 2013. Data errors for each plot caused by logger malfunction and operator mistakes were discarded, and the average hourly temperatures of the five plots for each treatment were used for analyses. In total, 18,396 average temperature values were obtained for each of OTCs and CONTs and 929 erroneous values were discarded. The date of snowmelt in 2011, 2012, and 2013, and snow depth at intervals of 1–10 days (from 28 January 2011 to 29 April 2012, and from 21 December 2012 to 19 April 2013) were recorded for each plot.

To monitor vegetative development immediately after snowmelt, species composition and vegetation cover were recorded in each plot at intervals of 1–4 weeks after snowmelt until mid-June when vegetation cover was approximately 100% (10, 10, and 9 censuses in 2011, 2012, and 2013, respectively). I recorded the number of species that living individuals (having green tissues) were observed as species richness within each plot. To estimate vegetation cover, I subdivided each plot into 100 10 cm × 10-cm subplots and visually evaluated plant cover of each subplot as 1% when plants occupied the whole area of the subplot or at intervals of 0.1% when plants occupied a partial area. The sum of the total cover of the 100 subplots was used to estimate vegetation cover in the plot. In 2013, the monitoring of vegetation was conducted in both plowed and unplowed areas within each plot. In mid- or late September of each year, when the vegetative height and aboveground biomass was approximately highest in the growing season, we sampled the aboveground plant parts in each plot. The sampling of each plot was conducted from a 1 m × 1-m area in 2011, a 20 cm × 1-m area in 2012, and a 20 cm × 1-m area of both plowed and unplowed areas in 2013. All samples were divided into species and weighed after drying at 70°C over 48 h. After sampling, all aboveground parts of plants in the plots were removed every year. I assumed that the aboveground removal had little effect on seed rain and plant growth because most plants had withered or nearly ended their reproduction and growth at harvest time.

Analysis

Data analysis was conducted using R (ver. 3.1.0.; R Development Core Team 2014). Using air temperature data, we compared the average monthly temperatures between CONTs and OTCs. We also calculated the difference in temperatures between CONTs and OTCs and averaged the difference for each hour. The differences were compared to zero using *t*-tests.

We analyzed repeated measures of species richness (number of species) and vegetation cover during early vegetative development after snowmelt using a generalized linear mixed-effects model (GLMM; the glmer function from the lme4 library in R). Species richness was analyzed with a Poisson error distribution to fit count data, and vegetation cover was analyzed with a binomial error distribution to fit proportion data. Models included warming/snow treatment (CONTs, OTCs, and SRs), plow treatment (plowed and unplowed), and their interaction as fixed effects. The GLMMs also included date of measurement and plot identity as random effects to take into account differences in richness and cover between censuses and temporal pseudoreplication by repeated measurements. All GLMMs were conducted using maximum likelihood estimation. The *p*-values for all GLMMs were calculated from the lmerTest library in R.

The biomass and species richness in September of each year were compared among treatments using Wilcoxon rank-sum tests.

Results

Air temperature was significantly elevated in OTCs. During the recording period, the average monthly temperature was 1.37°C higher in OTCs than in CONTs (Fig. 1a). The difference was statistically significant (*t*-test, $t = 14.8$, $p < 0.0001$). Warming was observed in the daytime between 06:00 and 18:00 (Fig. 1b, *t*-test, $t = 4.1$, $p < 0.0001$). The snowmelt date was 22, 26, and 16 days earlier in OTCs than in CONTs in 2011, 2012, and 2013, respectively. Average winter snow depth was greater in CONTs (55 cm in 2011 and 51 cm in 2012) than in OTCs (22 cm in 2011 and 21 cm in 2012). No snowdrifts were observed in OTCs. Maximum snow depth reached 89 cm in CONTs and 65 cm in OTCs during the 2011 winter and 97 cm in CONTs, 66 cm in OTCs, and 92 cm in SRs during the 2012 winter.

In the study grassland, all aboveground plant parts naturally withered during winter, whereas plants germinated from seeds or regrew from roots in every spring after snowmelt. Consequently the number of species and vegetation cover in all plots gradually increased with the progress of growing seasons. The combination of warming and early snowmelt led to earlier development of vegetation in OTCs than in CONTs. Species richness (number of species) was significantly higher in OTCs than in CONTs in the 3 years (Table 1A, Fig. 2a–d). Vegetation cover was also significantly higher in OTCs than in CONTs during the period between snowmelt and early June in 2012 and 2013 (Table 1B, Fig. 2e–h). Differences in vegetation cover between OTCs and CONTs disappeared by mid-June in 2011 and 2013, but remained in 2012 (Fig. 2). In contrast, temporal patterns of vegetation development were very similar between CONTs and SRs (Fig. 2). Therefore, no significant differences in species richness and vegetation cover were observed between CONTs and SRs in 2012 and 2013

(Table 1). When including accumulative temperature after snowmelt as a fixed effect, few significant differences in species richness and vegetation cover were detected between OTCs and CONTs and between SRs and CONTs (ESM1, 2), except species richness in 2013 between OTCs and CONTs and vegetation cover in 2012 between SRs and CONTs. Accumulative temperature had significant effects on richness and cover in the 3 years (ESM2).

Vegetation development was substantially diminished in plowed areas of the plots (Fig. 2d, h). The effects of plowing on species richness and vegetation cover were statistically significant in 2013 (Table 1). Moreover, a significant interaction was noted between the SR treatment and plowing on species richness (Table 1). In the models including accumulative temperature as a fixed effect, the effects of plowing, the interaction between the SR treatment and plowing on species richness, and the interaction between the OTC treatment and plowing on vegetation cover were all significant (ESM2).

Biomass and species richness tended to be highest in OTCs compared to SRs and CONTs in mid- or late September of each year, when vegetative height and aboveground biomass were approximately highest during the growing season. These differences were statistically significant for biomass between OTCs and SRs in 2012 and for species richness between OTCs and CONTs in 2011, between OTCs and SRs in 2012, and between OTCs and CONTs in unplowed areas in 2013 ($p < 0.05$, Wilcoxon rank-sum tests; Fig. 3).

Discussion

This study demonstrated the combined effects of snowmelt timing and warming on grassland vegetation in a cool temperate region. Early snowmelt enhanced vegetative growth when accompanied by warming (OTCs), but not under natural low air-temperatures (SRs). However, late snowmelt resulted in rapid vegetative growth under natural warm air-temperatures (CONTs). In general, early snowmelt leads to a prolonged growing season, and vegetation development is enhanced by the accompanying warm temperatures after snowmelt.

Compared to CONTs, OTCs had higher temperatures (average 1.37°C higher) and earlier snowmelt (16–26 days earlier). OTCs had 3.8 more species and 14.8% more vegetation cover than CONTs throughout the early growing seasons (from March to June after snowmelt). The increased vegetation development in OTCs was maintained until the end of the growing season (4.8 more species and 14.4% increase in biomass by September). The strong response of the grassland community to experimental warming was likely to have been caused by the characteristics of a cold and productive ecosystem. A meta-analysis of experimental warming at 32 research sites showed a greater positive response to warming in colder ecosystems (Rustad et al. 2001). The grassland studied here was exposed to generally low temperatures ranging from an average of 19.4°C in August to –5.6°C in February. Hudson and Henry (2010) suggested that plant communities dominated by unproductive and conservative species have a high resistance (low response) to climate change. In contrast, the grassland studied here was dominated by the pampass grass, *M. sinensis*, which has high productivity even in high-stress environments (Stewart et al. 2009). Therefore, productive communities in cold temperate regions should show the same or even larger responses to warming compared to arctic and alpine communities. A decrease in species diversity under warming has often been observed in arctic regions, mostly due to a decrease in the abundance and diversity of bryophytes (Wahren et al. 2005; Walker et al. 2006; Carbognarni et al. 2012). However, no bryophytes were recorded in this study. Warming leads to drought stress, causing a decrease in productivity (De Boeck et al. 2007) and diversity (Klein et al. 2004; Yang et al. 2011). Although no data on soil moisture were recorded during the study period, I recently measured soil moisture after snowmelt in April 2014, and observed no difference between OTCs and CONTs (R.O. Suzuki unpublished data). Conversely, clear differences were observed in the structure of local vegetation within hollow areas, in which precipitation and melted snow tended to accumulate (R.O. Suzuki personal observation), suggesting that higher soil water content may have had a greater impact on vegetation in the grassland than drought stress.

The advanced development of vegetation in OTCs was likely due to the combined effects of warming and early snowmelt. GLMM analyses indicated that the differences in species richness and vegetation cover between OTCs and CONTs disappeared when accumulative temperatures after snowmelt were included as a fixed effect, suggesting that vegetation responded in a similar manner to air temperatures irrespective of the treatment. Vegetative development might begin when a certain threshold temperature is surpassed (Rumpf et al. 2014). Therefore, early snowmelt advanced the start of growing seasons and warm air-temperature allowed plants to grow immediately after snowmelt in OTCs. However, the degree of enhanced vegetative growth in OTCs diminished over time in terms of biomass (1.37, 1.30, and 1.20 times larger in OTCs than in CONTs in 2011, 2012, and 2013, respectively) and plant height (1.14, 1.13, and 1.09 times larger in OTCs than in CONTs in 2011, 2012, and 2013, respectively; R.O. Suzuki unpublished data). A reduction effect on growth in OTCs has also been observed in arctic and alpine areas, in which the warming effect on plant growth diminished as plants exhausted stored resources (Arft et al. 1999; Hudson et al. 2011).

In SRs, early snow removal did not accelerate vegetation development. GLMM analyses revealed no differences in species richness and vegetation cover between CONTs and SRs. These results suggest that vegetation development in SRs was delayed until the time that snowmelt occurred in CONTs. This delayed development is likely to be due to cold air-temperatures after snow removal. A longer time would have been needed under colder temperatures to reach a threshold temperature for the initiation of vegetative development. In contrast, warm air-temperatures after natural snowmelt led to immediate vegetative growth in CONTs. Therefore, air temperature after snowmelt effectively determined the initiation of vegetative growth. Another possible explanation for the delayed development observed in SRs may be that the extra soil water from melted snow could have suppressed plant growth. Recent measurements of soil moisture immediately after snowmelt in April 2014 showed significant higher soil water in SRs than OTCs (R.O. Suzuki unpublished data). Furthermore, species richness and biomass in SRs were also similar to those in CONTs at the end of the growing season, suggesting that a prolonged growing season by early snow removal did not enhance vegetation growth throughout the growing season. Compared to the small number of other experiments involving snow removal, a large amount of evidence indicates that snow addition reduces plant productivity (Wipf & Rixen 2010), although the response to snow manipulation is species-dependent (Rumpf et al. 2014). This study demonstrated that snow removal might have only minor effects on plant productivity and diversity.

The overall effect of soil disturbance (plowing) was a reduction in species richness and productivity, irrespective of warming and snow removal treatments. As the consequence, differences in species richness and plant cover among treatments were substantially reduced in plowed areas. These results are consistent with previous evidence that aboveground disturbance by grazing dampens the effects of warming (Klein et al. 2004, Post and Pedersen 2008). I also found an interaction effect between plowing and the warming/snowmelt treatment. Compared to CONTs, species richness in SRs was higher in unplowed areas, but lower in plowed areas. The interaction effect might indicate that vegetation in SRs required a longer period to recover from soil disturbance than that in CONTs because plants in SRs were exposed to cold temperatures after snowmelt or that belowground parts were less protected from cold air-temperatures in plowed areas.

This study has several limitations. OTCs have various side effects, such as wind protection (Marion et al. 1997; Bokhorst et al. 2013). The effects of wind often alter plant phenology, morphology, and reduce plant growth (Whitehead 1962; Fukuyo et al. 1998). Although plants can show adaptive responses to wind stress by altering their morphological and physiological characteristics (Lawton 1982), the morphological and physiological response to wind decreases at low temperatures, suggesting an interaction effect of wind and temperature (Hunt and Jaffe 1980). Therefore, an interaction effect of wind shielding and warming is likely to enhance plant growth in OTCs. In addition, snow depth in OTCs was lower than in CONTs throughout winter, which may have resulted from the architectural structure of OTCs that prevent snowfall in the chambers and not due to warming. Differences in snow depth can cause differences in vegetative development by altering the soil temperature, soil nutrient availability, and frequency of freeze–thaw events (Decker et al. 2003; Wahren et al. 2005). However, Wipf et al. (2009) demonstrated that snowmelt timing had stronger effects on plant phenology and growth than snow depth.

Warming and early snowmelt can alter community structures, such as species composition (Schöb et al. 2009), species hierarchy (Harte & Shaw 1995; Klanderud & Totland 2005), and species interactions (Klanderud 2005). The short-term response of vegetation to warming often differs from the long-term response (Arft et al. 1999; Hudson and Henry 2010). Therefore, the rapid vegetation response observed in OTCs in this study might result in unpredictable changes in the community structures, such as an increase in invasive species (Dukes and Mooney 1999) and plant pathogens (Roy et al. 2004), causing a decline in species diversity during long-term warming. Future studies are required to evaluate the changes in species composition, species hierarchy, and responses of individual species to warming and earlier snowmelt during short- and long-term warming.

In conclusion, this study demonstrated that a combination of warming and early snowmelt largely enhances the development of vegetation, but the response is diminished when the soil is disturbed. Although climate change has been reported to have a strong impact on arctic and alpine ecosystems (Aerts et al. 2006; Elmendorf et al. 2012), present data suggest that the impact may also be substantial in temperate regions.

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References

Aerts R, Cornelissen JHC, Dorrepaal E, van Logtestijn RSP, Callaghan TV (2004) Effects of experimentally imposed climate scenarios on flowering phenology and flower production of subarctic bog species. Glob Change Biol 10:1599-1609 doi: 10.1111/j.1365-2486.2004.00815.x

Aerts R, Cornelissen JHC, Dorrepaal E (2006) Plant performance in a warmer world: general responses of plants from cold, northern biomes and the importance of winter and spring events. Plant Ecol:65-77 doi: 10.1007/s11258-005-9031-1

Arft A, Walker M, Gurevitch J (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. Ecol Monogr 69:491-511 doi: 10.1890/0012-9615(1999)069[0491:ROTPTE]2.0.CO;2

Bannister P, Maegli T, Dickinson KJM, Halloy SRP, Knight A, Lord JM, Mark AF, Spencer KL (2005) Will loss of snow cover during climatic warming expose New Zealand alpine plants to increased frost damage? Oecologia 144:245-256 doi: 10.1007/s00442-005-0087-3

Baptist F, Flahaut C, Streb P, Choler P (2010) No increase in alpine snowbed productivity in response to experimental lengthening of the growing season. Plant Biol 12:755-764 doi:

10.1111/j.1438-8677.2009.00286.x

Barnett TP, Adam JC, Lettenmaier DP (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303-309 doi: 10.1038/nature04141

Bokhorst S, Huiskes A, Aerts R, Convey P, Cooper EJ, Dalen L, Erschbamer B, Gudmundsson J, Hofgaard A, Hollister RD, Johnstone J, Jónsdóttir IS, Lebouvier M, Van de Vijver B, Wahren C-H, Dorrepaal E (2013) Variable temperature effects of Open Top Chambers at polar and alpine sites explained by irradiance and snow depth. Glob Change Biol 19:64-74 doi: 10.1111/gcb.12028

Carbognani M, Petraglia A, Tomaselli M (2012) Influence of snowmelt time on species richness, density and production in a late snowbed community. Acta Oecol 43:113-120 doi: 10.1016/j.actao.2012.06.003

De Boeck HJ, Lemmens CMHM, Gielen B, Bossuyt H, Malchair S, Carnol M, Merckx R, Ceulemans R, Nijs I (2007) Combined effects of climate warming and plant diversity loss on above- and below-ground grassland productivity. Environ Exp Bot 60:95-104 doi: 10.1016/j.envexpbot.2006.07.001

Decker K, Wang D, C. Waite, Scherbatskoy T (2003) Snow removal and ambient air temperature effects on forest soil temperatures in northern Vermont. Soil Sci Soc Am J 67:1234-1243 doi: 10.2136/sssaj2003.1234

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders ? Trends in Ecol Evol 14:135-139.

Elmendorf SC, Henry GHR, Hollister RD, Björk RG, Bjorkman AD, Callaghan TV, Collier

LS, Cooper EJ, Cornelissen JHC, Day TA, Fosaa AM, Gould WA, Grétarsdóttir J, Harte J, Hermanutz L, Hik DS, Hofgaard A, Jarrad F, Jónsdóttir IS, Keuper F, Klanderud K, Klein JA, Koh S, Kudo G, Lang SI, Loewen V, May JL, Mercado J, Michelsen A, Molau U, Myers-Smith IH, Oberbauer SF, Pieper S, Post E, Rixen C, Robinson CH, Schmidt NM, Shaver GR, Stenström A, Tolvanen A, Totland Ø, Troxler T, Wahren C-H, Webber PJ, Welker JM, Wookey PA (2012) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecol Lett 15:164-175 doi: 10.1111/j.1461-0248.2011.01716.x

Fukuyo S, Kurihara M, Nakashinden I, Kimura K, Iijima Y, Kobayashi Y, Masuzawa T, Yamamoto S, Morimoto M, Kouyama T, Kobayashi S, Yamamoto T, Mizuno K, Machida H (1998) Short-term effects of wind shield on phenology and growth of alpine plants in mount Kiso-komagatake, central japan (19th symposium on polar biology). Proc NIPR Symp Polar Biol 11:147-158.

Galen C, Stanton ML (1995) Responses of snowbed plant species to changes in growing-season length. Ecology 76:1546-1557.

Grime JP, Brown VK, Thompson K, Masters GJ, Hillier SH, Clarke IP, Askew AP, Corker D, Kielty JP (2000) The Response of two contrasting limestone grasslands to simulated climate change. Science 289:762-765 doi: 10.1126/science.289.5480.762

Gu L, Hanson PJ, Post WM, Kaiser DP, Yang B, Nemani R, Pallardy SG, Meyers T (2008) The 2007 eastern US spring freeze: increased cold damage in a warming world. BioScience 58:253-262 doi: 10.1641/B580311

Hannah L, Carr J, Lankerani A (1995) Human disturbance and natural habitat: a biome level analysis of a global data set. Biodivers Conserv 4:128-155 doi: 10.1007/BF00137781

Harte J, Shaw R (1995) Shifting dominance within a montane vegetation community: results of a climate-warming experiment. Science 267:876-880 doi: 10.1126/science.267.5199.876

Hegland SJ, Nielsen A, Lázaro A, Bjerknes A-L, Totland Ø (2009) How does climate warming affect plant-pollinator interactions? Ecol Lett 12:184-195 doi: 10.1111/j.1461-0248.2008.01269.x

Henry GHR, Molau U (1997) Tundra plants and climate change: the International Tundra Experiment (ITEX). Glob Change Biol 3:1-9 doi: 10.1111/j.1365-2486.1997.gcb132.x

Hudson JMG, Henry GHR (2010) High Arctic plant community resists 15 years of experimental warming. J Ecol 98: 1035-1041 doi: 10.1111/j.1365-2745.2010.01690.x

Hudson JMG, Henry GHR, Cornwell WK (2011) Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. Glob Change Biol 17:1013-1021 doi: 10.1111/j.1365-2486.2010.02294.x

Hülber K, Bardy K, Dullinger S (2011) Effects of snowmelt timing and competition on the performance of alpine snowbed plants. Perspect Plant Ecol Evol Syst 13:15-26.

Hunt ER. Jaffe MJ (1980) Thigmomorphogenesis: the interaction of wind and temperature in the field on the growth of *Phaseolus vulgaris* L. Ann Bot-London 45:665-672.

IPCC (2013) Climate change 2013: the physical science basis. contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Inouye D (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353-362 doi: 10.1890/06-2128.1

Klanderud K (2005) Climate change effects on species interactions in an alpine plant community. J Ecol 93:127-137 doi: 10.1111/j.1365-2745.2004.00944.x

Klanderud K, Totland Ø (2005) Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. Ecology 86:2047-2054 doi: 10.1890/04-1563

Klein J.A., Harte J, Zhao X-Q (2004) Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. Ecol Lett 7:1170-1179 doi: 10.1111/j.1461-0248.2004.00677.x

Kudo G, Nishikawa Y, Kasagi T, Kosuge S (2004) Does seed production of spring ephemerals decrease when spring comes early? Ecol Res 19:255-259 doi: 10.1111/j.1440-1703.2003.00630.x

Kudo G, Ida TY, Tani T (2008) Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants. Ecology 89:321-331 doi: 10.1890/06-2131.1

Lawton RO (1982) Wind stress and elfin stature in a montane rain forest tree: an adaptive explanation. Am J Bot 69:1224-1230.

Marion GM, Henry GHR, Freckman DW, Johnstone J, Jones G, Jones MH, Levesque E, Molau U, Molgaard P, Parsons AN, Svoboda J, Virginia RA (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. Glob Change Biol 3:20-32 doi: 10.1111/j.1365-2486.1997.gcb136.x

Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. Proc Natl Acad Sci USA 105: 12353-12358 doi: 10.1073/pnas.0802421105

R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Roy BA, Güsewell S, Harte J (2004) Response of plant pathogens and herbivores to a warming experiment. Ecology 85:2570-2581 doi: 10.1890/03-0182

Rumpf SB, Semenchuk PR, Dullinger S, Cooper EJ (2014) Idiosyncratic Responses of High Arctic Plants to Changing Snow Regimes. PLoS ONE 9: e86281. doi:10.1371/journal.pone.0086281

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J, GCTE-NEWS (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543-562 doi: 10.1007/s004420000544

Schöb C, Kammer PM, Choler P, Veit H (2009) Small-scale plant species distribution in snowbeds and its sensitivity to climate change. Plant Ecol 200:91-104 doi: 10.1007/s11258-008-9435-9

Semenchuk PR, Elberling B, Cooper EJ (2013) Snow cover and extreme winter warming events control flower abundance of some, but not all species in high arctic Svalbard. Ecol Evol 3: 2586-2599. doi:10.1002/ece3.648

Stewart JR, Toma Y, Fernández FG, Nishiwaki A, Yamada T, Bollero G (2009). The ecology and agronomy of *Miscanthus sinensis*, a species important to bioenergy crop development, in its native range in Japan: a review. GCB Bioenergy 1:126-153 doi: 10.1111/j.1757-1707.2009.01010.x

Totland Ø, Alatalo JM (2002) Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis*. Oecologia 133:168-175 doi: 10.1007/s00442-002-1028-z

Wahren C-H A., Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. Glob Change Biol 11:537-552 doi: 10.1111/j.1365-2486.2005.00927.x

Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carroll AB, Epstein HE, Jónsdóttir IS, Klein J a, Magnússon B, Molau U, Oberbauer SF, Rewa SP, Robinson CH, Shaver GR, Suding KN, Thompson CC, Tolvanen A, Totland Ø, Turner PL, Tweedie CE, Webber PJ, Wookey PA (2006) Plant community responses to experimental warming across the tundra biome. Proc Natl Acad Sci USA 103:1342-1346 doi: 10.1073/pnas.0503198103

Whitehead FH (1962) Experimental studies of the effect of wind on plant growth and anatomy. New Phytol 61:59-62 doi: 10.1111/j.1469-8137.1962.tb06274.x

Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. Climatic Change 94:105-121 doi: 10.1007/s10584-009-9546-x

Wipf S, Rixen C (2010) A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. Polar Research 29:95-109 doi: 10.1111/j.1751-8369.2010.00153.x

Yang H, Wu M, Liu W, Zhang Z, Zhang N, Wan S (2011) Community structure and composition in response to climate change in a temperate steppe. Glob Change Biol 17:452-465 doi: 10.1111/j.1365-2486.2010.02253.x

Yasunari T, Ueno K (1987) The snow cover environment in Sugadaira, central Japan. Ann Rep Inst Geosci Univ Tsukuba 13:58-64.

Figure legends

Plate 1 Open-top chambers (OTCs) used in this study. OTCs were produced using stainless steel frames and corrugated, acrylic-transparent panels of 2 m height and 1 m width that surrounded all lateral sides. The top and a region 10 cm above ground were opened in each OTC.

Fig. 1 Variations in the average monthly temperatures (a) in control plots (CONTs; mean, open circle; SD, dashed line) and warming plots using open-top chambers (OTCs; mean, closed circle; SD, dotted line) and the differences in temperatures (b) for each hour between CONTs and OTCs.

Fig. 2 Temporal changes in plant species richness (number of species) and vegetation cover (%) in 2011, 2012, and 2013 (mean ± SD). In 2011, warming plots using open-top chambers (OTCs, *closed circle*) and control plots (CONTs, *open circle*) were established. In 2012, plots with snow removal (SRs, *open square*) at the time of snowmelt within OTCs were added. In 2013, half of the area of all plots were plowed to disturb the vegetation.

Fig. 3 Above-ground biomass and species richness in three treatments at September of three years when vegetative height and biomass was approximately highest in a growing season (mean + SD): OTC, warming plots using open-top chambers; CONT, control plots; SR, plots with snow removal. Sampling of each plot was performed from a 1 m × 1 m area in 2011, a 20 cm × 1 m area in 2012, and a 20 cm × 1 m area of each plowed and unplowed area in 2013.

Different letters indicate significant differences among treatments ($P < 0.05$, Wilcoxon rank sum tests).

Plate 1

Fig. 1

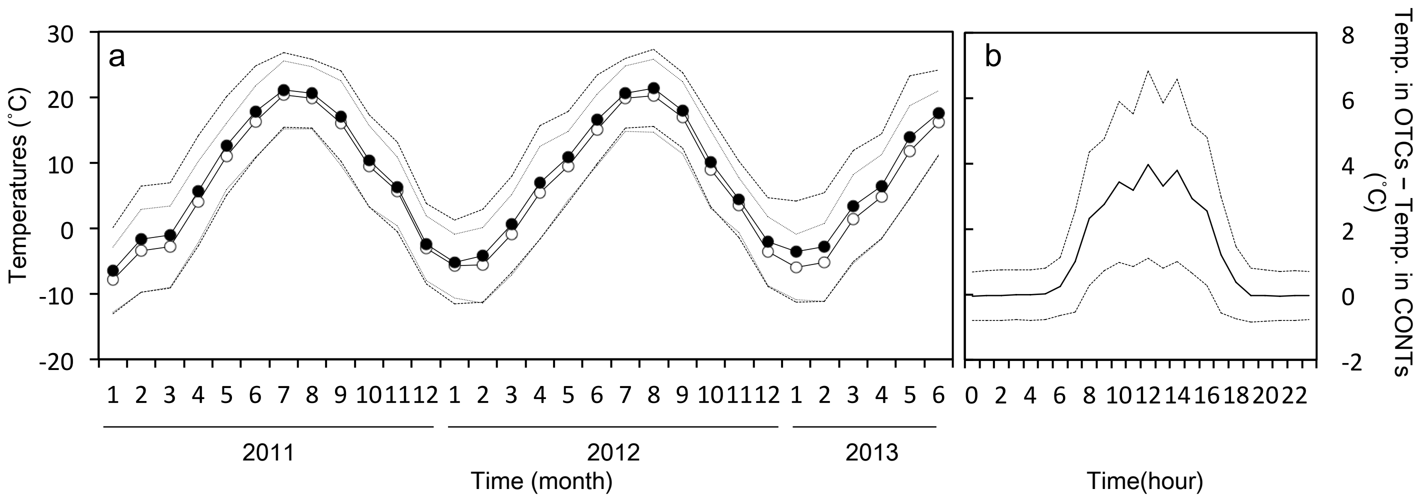

a
b
30
20
10
0
-10
-20
Temperatures (˚C)
8
6
4
2
0
-2
Temp. in OTCs – Temp. in CONTs (˚C)
1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6
2011
2012
2013
Time (month)
0 2 4 6 8 10 12 14 16 18 20 22
Time(hour)

Fig. 2

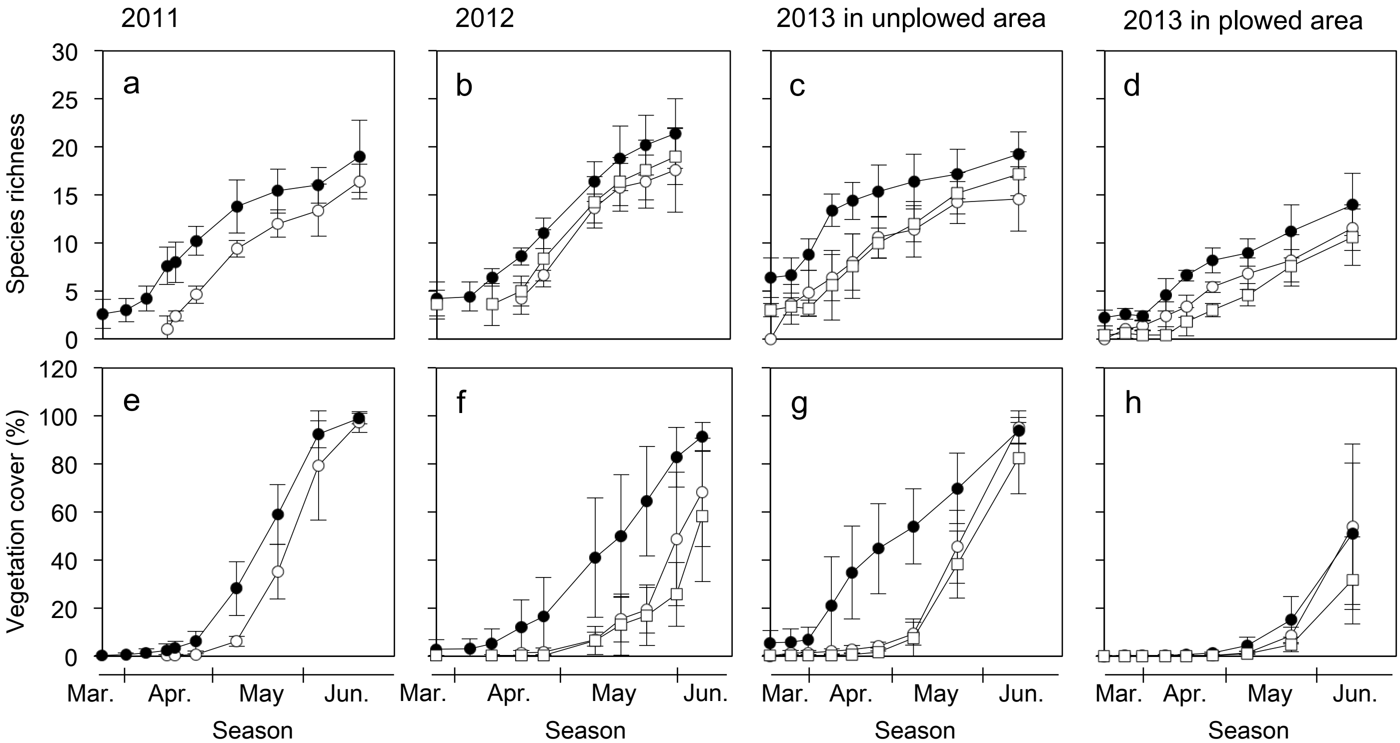

2011
2012
2013 in unplowed area
2013 in plowed area
Species richness
Vegetation cover (%)
a
b
c
d
e
f
g
h
0
5
10
15
20
25
30
0
20
40
60
80
100
120
Mar.
Apr.
May
Jun.
Season

Fig. 3

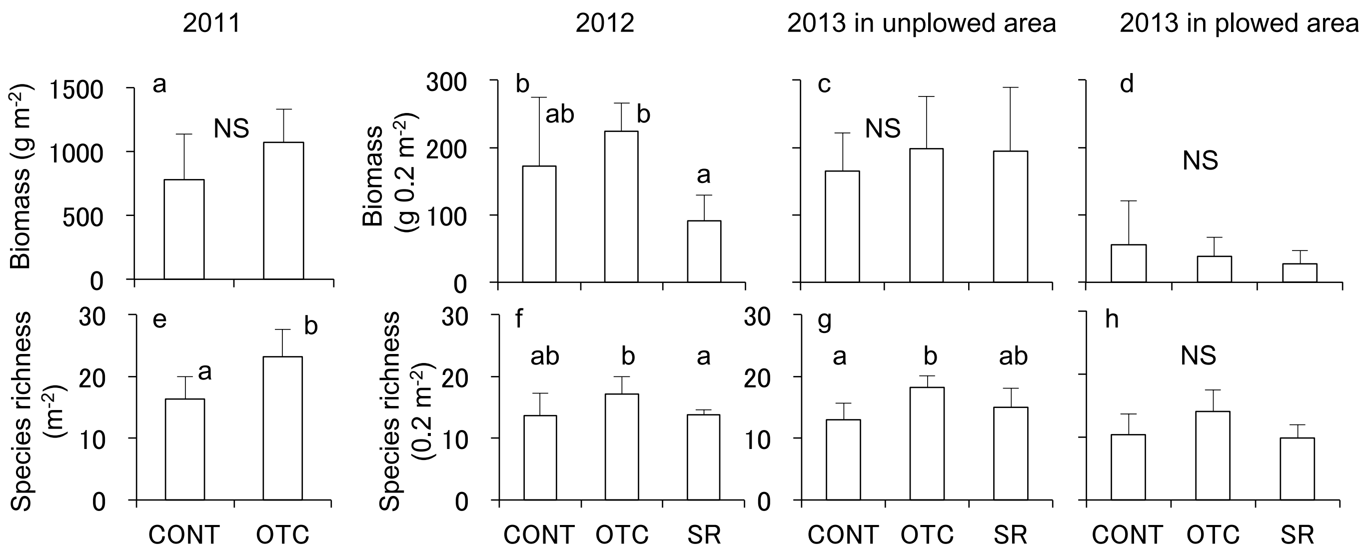
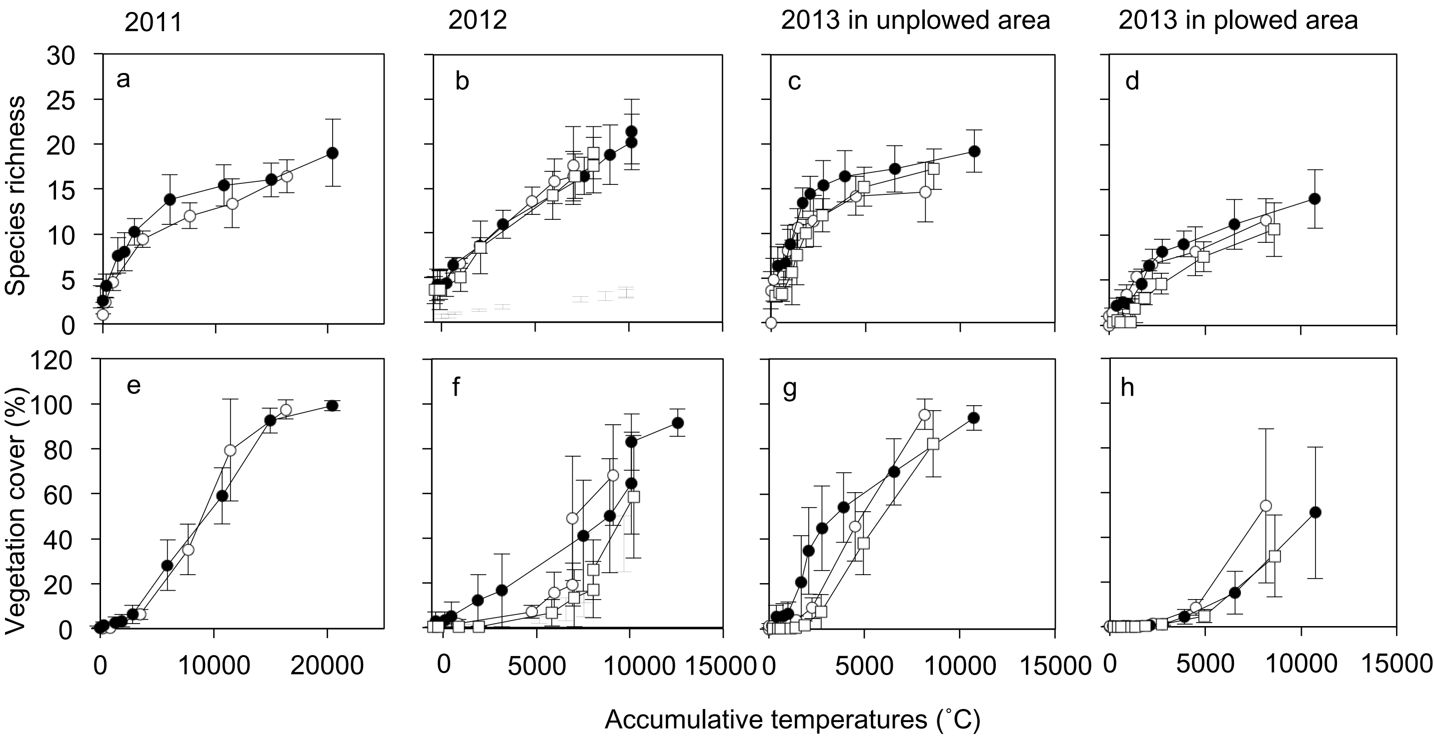

2011
2012
2013 in unplowed area
2013 in plowed area
Biomass (g m-2)
Biomass (g 0.2 m-2)
1500
1000
500
0
300
200
100
a
b
c
d
NS
ab
Species richness (m-2)
Species richness (0.2 m-2)
30
20
10
e
f
g
h
CONT
OTC
SR

Table 1 Results of the generalized linear mixed-effects model testing the effects of treatments and days after snowmelt on plant species richness (A) and vegetation cover (B) during study periods in 2011, 2012, and 2013. Models included date of measurement and plot identity as random effects. The bold value indicates statistical significant.

	2011			2012			2013		
(A) species richness	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	1.72	0.23	**<0.0001**	2.06	0.23	**<0.0001**	1.42	0.08	**<0.0001**
Treat. OTC	0.36	0.09	**<0.0001**	0.26	0.09	**0.0051**	0.42	0.09	**<0.0001**
Treat. Snow removal				0.07	0.10	0.4792	0.00	0.10	0.9794
Plow (P)							-0.60	0.09	**<0.0001**
Treat. OTC x P							-0.06	0.11	0.6152
Treat. Snow removal x P							-0.36	0.13	**0.0058**
(B) vegetation cover	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-3.78	1.39	**0.0067**	-3.57	0.94	**0.0001**	-3.29	1.25	**0.0084**
Treat. OTC	1.13	0.83	0.1758	2.30	0.72	**0.0013**	2.58	0.91	**0.0046**
Treat. Snow removal				-1.46	0.85	0.0848	-1.37	1.05	0.1937
Plow (P)							-3.38	1.30	**0.0093**
Treat. OTC x P							-2.59	1.46	0.0760
Treat. Snow removal x P							-0.45	1.81	0.8021

SE: Standard error of estimate values.

ESM1



ESM1 Relationships with accumulative temperatures after snowmelt in OTCs to plant species richness (number of species) and vegetation cover (%) in 2011, 2012, and 2013 (mean ± SD). In 2011, warming plots using open-top chambers (OTCs, *closed circle*) and control plots (CONTs, *open circle*) were established. In 2012, plots with snow removal (SRs, *open square*) at the time of snowmelt within OTCs were added. In 2013, half of the area of all plots were plowed to disturb vegetation.

ESM2 Results of the generalized linear mixed-effects model testing the effects of treatments and accumulative temperature on plant species richness (A) and vegetation cover (B) during study periods in 2011, 2012, and 2013. Models included date of measurement and plot identity as random effects. Accumulative temperature was calculated as summing the average hour temperature in each treatment during a period from the snowmelt date to the day before the census date.

	2011			2012			2013		
(A) species richness	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	1.53	0.13	**<0.0001**	1.74	0.08	**<0.0001**	2.46	0.46	**<0.0001**
Accumulative temperature *1	0.08	0.01	**<0.0001**	0.15	0.01	**<0.0001**	-0.27	0.07	**<0.0001**
Treat. OTC	0.12	0.10	0.2430	-0.18	0.09	0.0508	0.88	0.15	**<0.0001**
Treat. Snow removal				-0.12	0.09	0.1963	0.14	0.11	0.1971
Plow (P)							-0.60	0.09	**<0.0001**
Treat. OTC x P							-0.06	0.11	0.6151
Treat. Snow removal x P							-0.36	0.13	**0.0058**
(B) vegetation cover	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Intercept	-8.92	3.22	**0.0057**	-13.15	3.10	**<0.0001**	-6.80	1.50	**<0.0001**
Accumulative temperature *1	0.93	0.33	**0.0042**	1.60	0.39	**<0.0001**	1.36	0.28	**<0.0001**
Treat. OTC	-0.68	1.27	0.5953	-1.93	1.16	0.0952	1.86	1.19	0.1173
Treat. Snow removal				-3.32	1.33	**0.0124**	-2.73	1.66	0.0998
Plow (P)							-3.74	1.63	**0.0219**
Treat. OTC x P							-5.41	2.01	**0.0072**
Treat. Snow removal x P							-0.07	2.08	0.9718

*: Estimate values and SE are multiplied by 1000 to be visible values. SE: Standard error of estimate values.